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Study of Gap-phase Regeneration in a Managed Beech Forest: Relations between Tree Regeneration and Light, Substrate Features and Cover of Ground Vegetation

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Abstract – Gap formation by wind is a characteristic disturbance event in European beech forests. Changes in abiotic environmental variables depend on gap size and different site features. The aim of this gap-study is to test the effect of gap size on spatial distribution of abiotic environmental variables and on the abundance and distribution of tree regeneration. Eight experimental gaps – three large (d: 35-40 m) and five small (d: 10-15 m) – were created in a mesotrophic beech forest in winter 2000/2001. Data were collected systematically in 1m x 1m quadrats before gap creation and subsequently on five occasions. Hemispherical photographs were used to estimate relative light intensity along a gap–under-canopy transect. First results of this long-term study suggest that establishment of beech seedlings is negatively influenced by dispersal limitation in large gaps and amount of slash as well, while it seems to be insensitive to environmental conditions. Development of beech saplings is accelerated by increased light intensity, and by protective effect of dense herb layer in opened sites. *Salix caprea* — as a light demanding species — appears mostly in the centre of large gaps.

artificial gap / PACL / *Fagus sylvatica*

Kivonat – A fás újulat vizsgálata kezelt bükkös erdő lékjeiben: az újulat valamint a fény, a talajfelszíni jellemzők és az aljnövényzeti borítás összefüggései. A széldöntés által kiváltott lékképződés jellemző bolygatási jelenség bükk által dominált erdőkben. A lékekben az abiotikus környezeti változók alakulása a lékmérettől és a termőhely különböző tényezőitől függ. A vizsgálat célja annak megállapítása, hogy a lékméret hogyan befolyásolja az abiotikus környezeti tényezők térbeli mintázatát, valamint a fás újulat tömegességi és térbeli viszonyait. Bükk által dominált állományban nyolc kísérleti léket hoztunk létre 2000/2001 telén: három nagyot (átm: 35-40 m), és öt kicsit (átm: 10-15 m). Az adatgyűjtés szisztematikus módon, 1m x 1m-es kvadrátok segítségével történt a léknyitást megelőzően, majd öt további felvétel során. A relatív megvilágítottság becsléséhez halszemoptikás felvételeket készítettünk a léken áthúzódó transzekt mentén. A vizsgálat első eredményei szerint a bükk felújulását nagy lélekben negatívan befolyásolja a magterjedés korlátozottsága, valamint a gallyak mennyisége, miközben a környezeti változók hatása csekély. A bükk fejlődését a fényintenzitás növekedése valamint a sűrű aljnövényzet védelme elősegíti. A kecskefűz, mint fényigényes faj leginkább a nagy lékek közepén jelenik meg.

mesterséges lék / PACL / *Fagus sylvatica*

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1 INTRODUCTION

In Hungarian beech forests formation of gaps by windthrow is a characteristic natural disturbance event. Other factors that can generate gaps: snow, fire, insects, fungi, etc. (Peterken 1996, Somogyi 1998). Resulting abiotic and biotic conditions can be very different both within individual gaps – depending on gap size – and among different sites (Canham 1989, Collins and Pickett 1987, Collins and Pickett 1988, Holeksa 2003, Kwit and Platt 2003, Nakashizuka 1985, Runkle 1989, Poulson and Platt 1989, Platt and Strong 1989, Vitousek and Denslow 1986, Denslow and Spies 1990). Consequently, it is not easy to predict how herbaceous and woody species react to gap formation.

Different explanations and theories have been published on how species establish and survive in gaps of different forest types all around the world. Theory of *gap partitioning* emphasizes the role of the resource gradients (e.g. light) from beneath intact canopy to the centre of the gap, which is too broad to be dominated by one species (Gray and Spies 1996). Establishment and growth of different tree species are therefore correlated with gap size and within-gap position (Brokaw and Busing 2000, Busing and White 1997). The *microsites as regeneration niches* concept emphasizes the role of specific substrates (e.g., logs, pits and mounds), which can be important as regeneration niches. Heterogeneity observed at the seedling scale (< 10 cm) often overrides larger-scale environmental gradients (>2 m) associated with gap size and within-gap position (Gray and Spies 1997).

This paper shows preliminary results of a long-term experiment focusing on gap-phase regeneration in a submontane beech forest in Hungary. The aim of our study is to investigate how gap size influences the spatial distribution of relative light intensity in gaps; the effect of relative light intensity, and pattern of substrate types on the distribution and abundance of regeneration of tree species.

Our questions are the following: 1. Are there any significant differences in the composition and abundance of regeneration species in small versus large gaps and within each gapsize class during the first 4 years? 2. How do environmental factors (total, direct and diffuse relative light intensity; proportions of substrate features) influence the occurrence and the abundance of tree species?

Although empirical observations and development of methods of natural regeneration using group selection are available already in historic forestry literature (e.g. Gayer 1895, Roth 1935), the lack of scientific data justified the initiation of experiments focusing on the impact of group selection in Hungarian beech forests. It is expected that the ongoing gap-experiments would provide valuable results for the forestry practice of this region.

2 MATERIALS AND METHODS

2.1 Study area

The study was carried out on the east-northeast-facing slope of the Szén-patak Valley in the Börzsöny Mountains, Northern Hungary (47.9°N, 18.9°E). Elevation is 540-610 m a.s.l., mean annual temperature is 8°C, mean monthly temperature is –3.5 °C and 18 °C in January and in July, respectively. Annual precipitation is 700-800 mm. Bedrock is andesite, on which medium deep brown forest soil has developed. The experimental stand belongs to the mesotrophic submontane beech forest type, in which beech *(Fagus sylvatica)* is monodominant, common ash *(Fraxinus excelsior)*, Norway maple *(Acer platanoides),* sycamore *(Acer pseudoplatanus),* field maple *(Acer campestre)*, lime *(Tilia cordata, Tilia platyphyllos)* and hornbeam *(Carpinus betulus)* are present in small amounts. The more or less homogeneous tree stand is approx. 80 years old with average tree height and dbh of 25 m, and 30 cm, respectively. Under the homogenous beech canopy, the herb layer is rather poor. The most abundant vascular species include *Mycelis muralis, Luzula luzuloides, Carex pilosa, Epilobium montanum, Mercurialis perennis, Hieracium sp., Athyrium filix-femina* and *Dryopteris filix-mas*. Spring geophytes are sparse. Game pressure is high, tree seedlings and saplings are greatly affected by intensive browsing. Advance regeneration (>1 m) is poor. The area has been under forestry management using shelterwood regeneration system for a long time. At present it is managed by Ipoly Erdő Co.

2.2 Methods

The location of eight circular artificial gaps – three large (diameter approx. 35-40 m, H:D, i.e. ratio of tree height of the surrounding canopy trees and diameter of gap = 1:1,5) and five small (diameter approx. 10-15 m, H:D = 1:0,5) – were selected in autumn 2000. Gaps were created after the first survey (August 2000) in February 2001. We used a systematic sampling design, with 5-meter grid resolution and 1 x 1 m quadrats. As *Figure 1* shows, each large gap contains 123 quadrats, whereas small gaps contain 64 quadrats each. We sampled each year 689 quadrats except in 2004, when every second quadrat (altogether 355) was sampled.

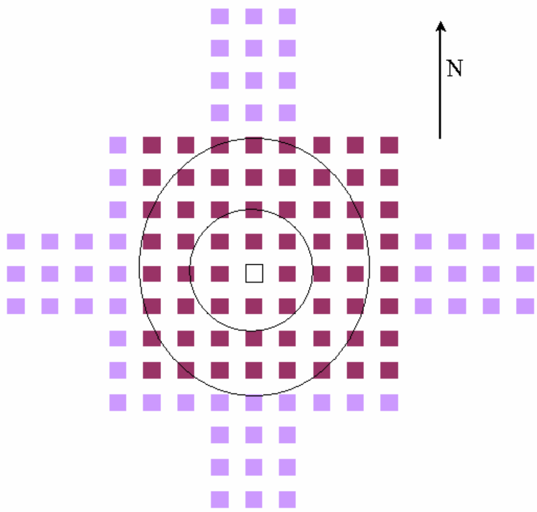


Figure 1. Sampling design in small (dark cells) and large gaps (light cells). 1x1 m quadrates are symbolised by filled rectangles, gaps are symbolised by circles. Distance between quadrats is 5 m.

Vegetation data were recorded on 6 occasions (in Sept.-Oct. 2000, May/Sept.-Oct. 2001, May/Sept.-Oct. 2002, Aug.-Sept. 2004). In each quadrat the following data were recorded: the number of individuals for all tree species in 4 size classes (0-10 cm, 10-20 cm, 20-50 cm, >50 cm) and the percent cover of each herbaceous species (including chamaephytons). On each occasion we determined the cover of each herbaceous species using visual estimation in each quadrate. C*overage of different substrate types* (intact soil, mineral soil, coarse woody debris–CWD, living tree stem or exposed root, stone) were recorded in spring 2001 and 2002 and autumn 2004 in each quadrat (*Figure 2*). *Hemispherical photographs* were taken at 70 cm height above ground in the sample quadrats along N-S, E-W transects. The transects crossed each other at the centre of the gaps. Alltogether 101 photos taken in 2002 were used to calculate relative light intensity (in Percent of Above Canopy Light, PACL). Photos were analysed using a Windows-based software, hemIMAGE developed by Andreas Brunner

(Brunner 2000). Relative light intensity (in PACL) was calculated for a given period of time in a certain location. With hemIMAGE the direct and the diffuse light can be calculated separately for a given point, assuming (based on meteorological data) that 0,5 of the Above Canopy Light (ACL) is the diffuse light component. We calculated the PACL for the period from March 1 to October 31. Different light intensity zones were distinguished within each gap based on diffuse PACL as follows: Z1 – 0-10% diffuse PACL (under canopy); Z2 – 10-20% diffuse PACL (in centre of small gaps and at the edge of large gaps); Z3- >20% diffuse PACL (in centre of large gaps). These zones were used for analysing species abundances.

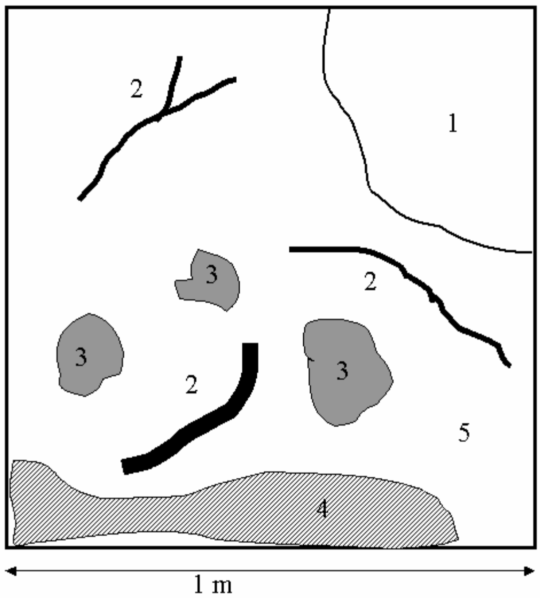


Figure 2. Registrated substrate types in each quadrate:
1: Living tree trunk or exposed root, 2: Coarse woody debris (CWD), 3: stone,
4: surfaces without litter cover (mineral soil), 5: intact soil (covered by litter, not disturbed)

Canonical correspondence analysis with Canoco for Windows 4.5 software was carried out as multivariate analysis of data in 2004. Abundance of tree species and abiotic variables recorded in quadrats (percent of intact soil, mineral soil, stone, tree, coarse woody debris, coverage of herbaceous plant species and light zones) were included in the analysis. *Nonparametric statistical analysis* – Mann-Whitney U test – was used to compare the recorded vegetation and environmental variables between small versus large gaps. Interactions between abiotic factors and species abundances recorded in 2004 were tested by calculating Spearman Rank Order correlation.

3 RESULTS

Results from hemispherical photo analyses show that under the homogeneous beech canopy relative light intensity in Percent of Above Canopy Light (PACL) for the given vegetation period is around 5-10% *(Table 1a, 1b)*. Small and large gaps are significantly ($p < 0,001$, Mann-Whitney U Test) different in terms of total, diffuse and direct PACL values. As *Tables 1a* and *b* show, their minimum values, characterising dense beech canopy, are similar, but maximum PACL values are different. In the centre of gaps much higher proportion of ACL reaches the ground in large gaps than in small ones (about 20% more, both with direct and diffuse light components). The light environment near the edges of large gaps is similar to the brightest part of small gaps.

Table 1a. Descriptive statistics of relative light intensity (in Percent of Above Canopy Light, PACL) in small gaps

	Valid N	Mean	Median	Minimum	Maximum	Range	Variance	Std.Dev.
DIRECT	56	6.8	4.4	1.4	19.8	18.4	0.2	4.9
DIFFUSE	56	10.3	9.9	4.5	16.4	11.9	0.1	3.2
TOTAL	56	8.6	8.5	3.9	14.8	10.9	0.1	2.6

Table 1b. Descriptive statistics of relative light intensity (in Percent of Above Canopy Light, PACL) in large gaps

	Valid N	Mean	Median	Minimum	Maximum	Range	Variance	Std.Dev.
DIRECT	50	14.2	8.7	0.7	39.3	21.8	1.5	12.1
DIFFUSE	50	19.2	18.3	5.0	36.4	19.9	1.2	10.8
TOTAL	50	16.7	16.1	3.8	34.6	17.7	0.9	9.7

On average, more diffuse light reaches the ground than direct sunlight from the sunbeams in most of the sample plots. However, it can vary in certain part of the gaps.

The pattern of diffuse PACL is influenced by the structure of the surrounding stand and it also reflects gap geometry. In the centre of small gaps diffuse PACL is ca. 15%, in large gaps diffuse PACL values vary between 30-36%. At the edges it is ca.10% in small and ca. 20-25% in large gaps. Relative light under canopy intensity decreases below 10% within 10-15 meters, i.e. 0,5*tree-height from the edge.

Direct sunlight reaches the ground for longer periods in the N, N-W part of the gaps during the whole growing season. In small gaps direct PACL reaches 15-19% in the N parts of the gap, in large gaps direct PACL can reach 32-36%.

Total cover of herbaceous species has shown considerable increase in 4 years *(Table 2).* The highest increase is characteristic in gap centres (both of large and small gaps). Most abundant herbaceous species were: *Atropa bella-donna, Carex remota, Cirsium arvense, Epilobium montanum, Fragaria vesca, Hypericum perforatum, Rubus fruticosus, Rubus idaeus, Scrophularia nodosa, Stachys sylvatica, Urtica dioica.*

Table 2. Mean cover (mean±st. err. in percents) *of quadrats in small and large gaps in different light zones at consecutive sampling dates. (Z1: light zone of 0-10% diffuse PACL, Z2: light zone of 10-20% diffuse PACL, Z3: light zone of 20%< diffuse PACL)*

	Small gaps Z1	Large gaps Z1	Small gaps Z2	Large gaps Z2	Large gaps Z3
No of samples	239 (117 in 2004)	113 (61 in 2004)	81 (43 in 2004)	115 (61 in 2004)	141 (73 in 2004)
2000 autumn	**0,3** ±0,1	**0,01** ±0,01	**0,03** ±0,02	**0,04** ±0,02	**0,01** ±0,01
2002 autumn	**3,0** ±0,7	**0,9** ±0,5	**22,9** ±3,9	**6,4** ±1,4	**42,3** ±3,2
2004 autumn	**3,5** ±0,9	**2,4** ±0,7	**33,8** ±5,4	**17,1** ±3,9	**52,3** ±4,7

Regeneration was very sparse in 2000 before gap creation, with little difference among gaps. Next year there was only a small development in number, but in autumn 2002 we found significant changes because of the beech mast in 2001 *(Figure 3).* As a consequence, in 2004 taller beech seedlings was found in relatively high number. Regeneration of other species (*e.g. Salix caprea, Fraxinus excelsior, Acer spp., Tilia ssp.*) was even sparser with stochastic differences among gaps and years. *Salix caprea* appeared in considerable amount in 2002, however, in 2004, only individuals of larger size classes (> 10 cm) were found in gaps.

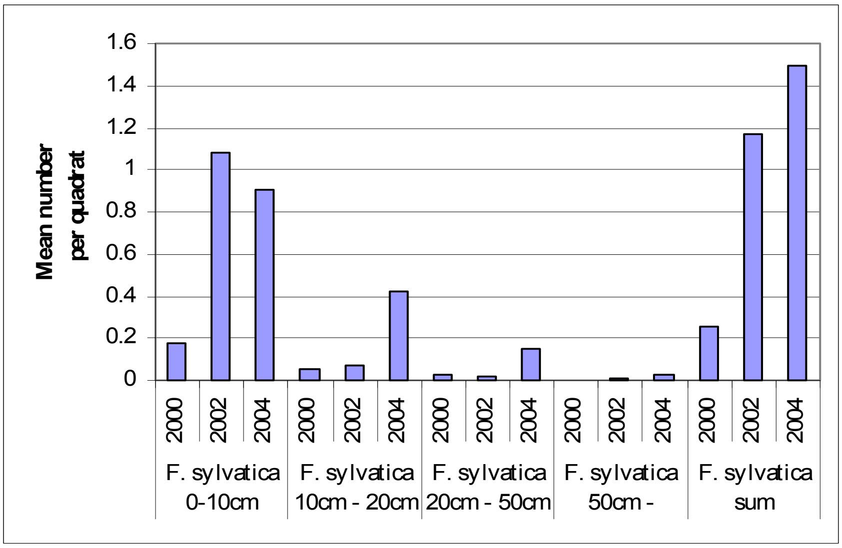


Figure 3. Mean number of beech individuals per quadrate (from all of the gaps) in 2000, 2002 and 2004

Canonical correspondence analysis (Figure 4) showed the relationship between abiotic and biotic variables for data of 2004. All abiotic variables (percent of intact soil, mineral soil, stone, tree, coarse woody debris, coverage of herbaceous plant species and light zones as nominal variables) were included in the model. The following variables were added to the model as significant variable: coverage of herbaceous species (plantsum) (explaining variance of 0,3 of 0,36 at $p = 0.002$, F-ratio = 29.10, number of permutations = 499), percentage of living tree basal area in quadrats (explaining variance of 0,02 of 0,36 at $p = 0.07$, F-ratio = 2.12; number of permutations = 499), Axis 1 and 2 cover the cumulative percentage variance of species-environment relation and 14 % of variance of species data. Axis 1 mostly correlates (0.99) with coverage of herbaceous species (plantsum), while axis 2 seems to be mostly determined by living tree basal area percent (0.99). According to the results among *Fagus sylvatica* seedlings and saplings, larger size classes show correlation with increasing plant coverage, together with *Salix caprea* saplings. Occurrence and coverage of living canopy trees correlates with *Fraxinus excelsior* saplings, while beech saplings between 10 and 20 cm mainly occur where canopy trees are not present.

Abundance of seedlings and saplings by size classes reflect different changes in the three light zones. There are significant – though adverse – changes in the abundance of small (<10 cm) seedlings,. There is an increase in seedling numbers regardless of the zones in both small and large gaps *(Figure 5a)*. Increase is much higher in case of small gaps. Results show similar pattern concerning the saplings between 10-20 cm *(Figure 5b)*. In case of saplings taller than 20 cm there is an extraordinary high increase (Mann-Whitney U Test, $p < 0.05$, see *Figures. 5c, 6.*) in the abundance in the brightest zone of large gaps (where diffuse PACL is above 20%). These individuals originate from small saplings of year 2000 (see *Figure 5a*). If plots in 2004 in gaps and under canopy are compared concerning gap size, our results show that in small gaps there is no difference in abundance of beech seedlings (<10 cm) between in-gap or under-canopy plots, while in large gaps amount of seedlings is lower in in-gap plots than under canopy plots (Mann Whitney U Test, $p = 0.03$).

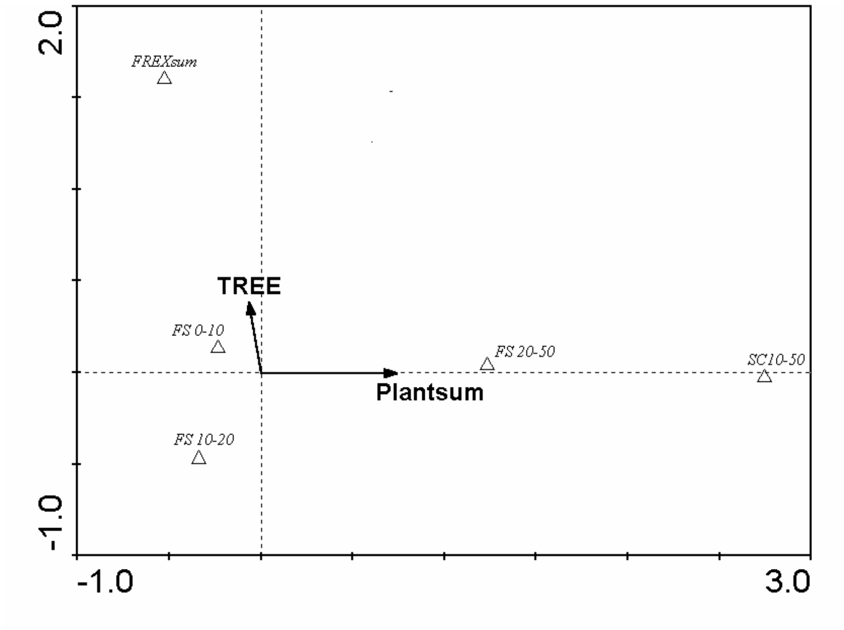


Figure 4. Canonical correspondence analysis for 2004 data.
(FS 0-10: Fagus sylvatica seedlings, <10 cm, FS10-20: Fagus sylvatica 10-20 cm,
FS20-50: Fagus sylvatica 20-50 cm, SC10-50: Salix caprea 10-50 cm,
TREE: coverage of living canopy tree stems in quadrats,
Plantsum: total cover of herbaceous plants)

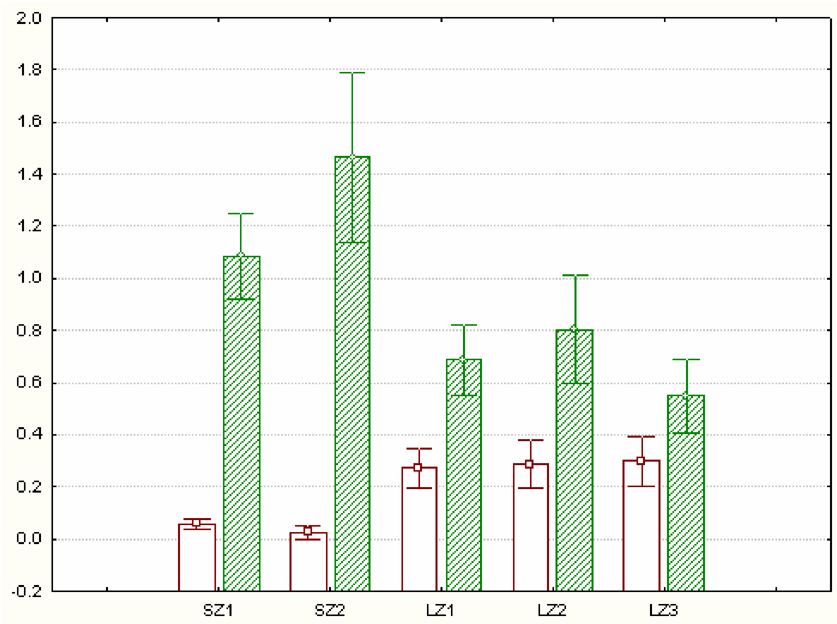


Figure 5a. Average number of Fagus sylvatica seedlings (0-10cm) per quadrat
according to light zones in small and large gaps in 2000 and in 2004.
*(Columns represent mean, whiskers represent ±1*SE., S: small gaps, L: large gaps, Z1-Z3: zones,*
empty columns: year 2000 , shaded columns: year 2004)

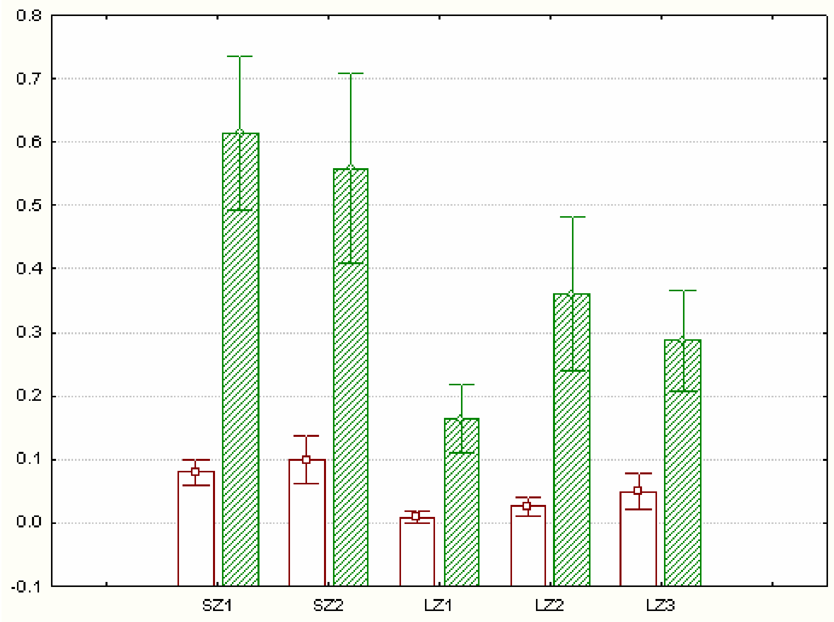


Figure 5b. Average number of Fagus sylvatica seedlings (10-20 cm) per quadrat according to light zones in small and large gaps in 2000 and in 2004. (For explanation see Figure 5a)

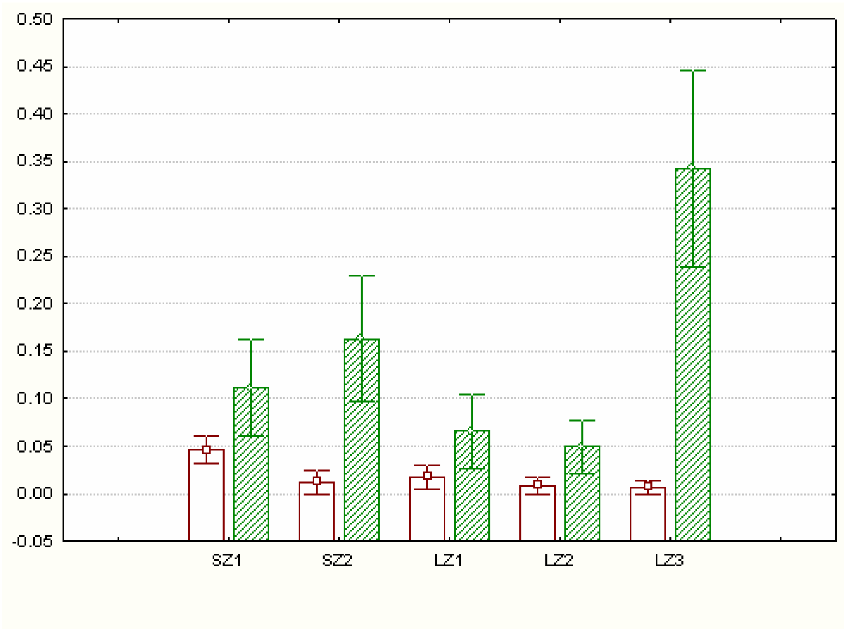


Figure 5c. Average number of Fagus sylvatica seedlings (20-50 cm) per quadrat according to light zones in small and large gaps gaps in 2000 and in 2004. (For explanation see Figure 5a)

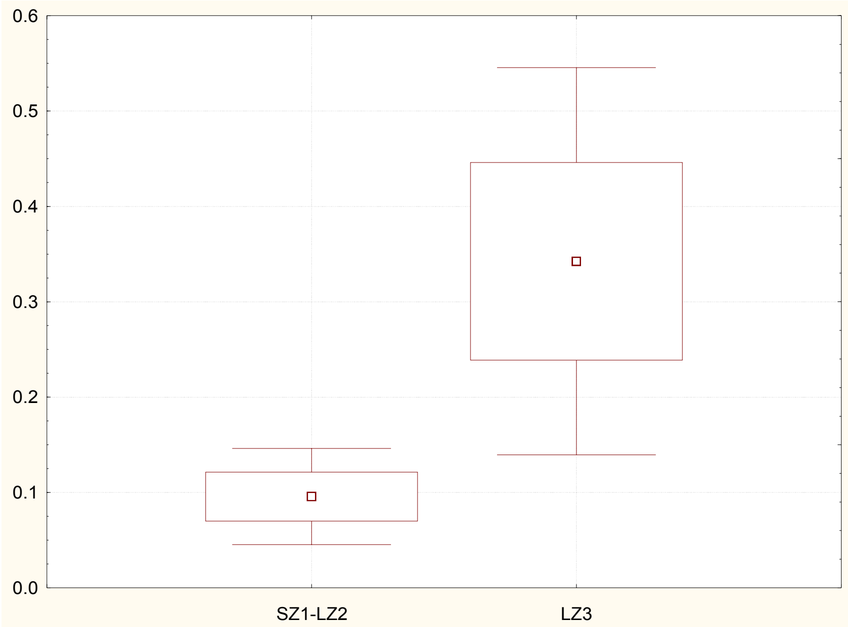


Figure 6. Average number of Fagus sylvatica saplings (20-50 cm) per quadrat in the Z1-Z2 and in Z3 light zone in 2004.
*(Centre of the box represents mean, box represents ± 1*SE, whisker represents ± 1,96*SE, SZ1-LZ2: Light zone Z1 and Z2 in small and large gaps together, LZ3: Light zone Z3 in large gaps)*

Salix caprea saplings occur only in gaps or at the edge of gaps regardless of gap size. They are most abundant in the centre of large gaps *(Figure 7)*, while there is also a considerable amount in the centre of small gaps.

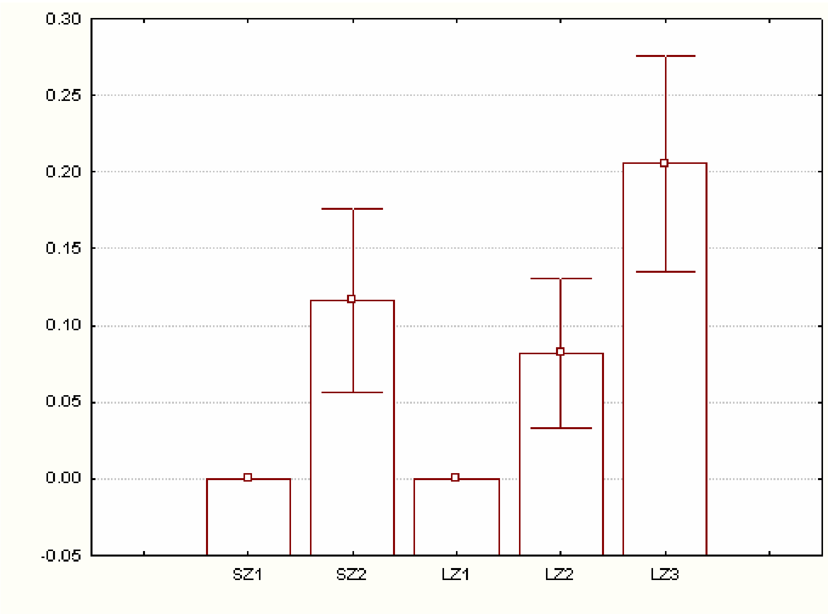


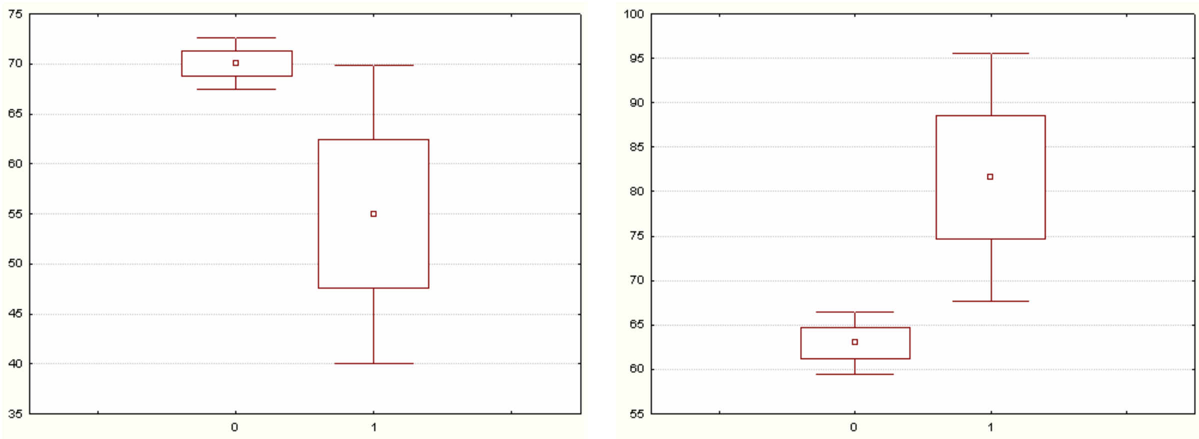
Figure 7. Average number of Salix caprea saplings per quadrat according to light zones in small and large gaps in 2004.
(For explanation see Figure 5a)

According to results of *correlation* analysis (Spearman Rank Order Correlations) *(Table 3)* small beech seedlings show weak negative correlation with coarse woody debris (CWD) and positive correlation with percent cover of stone. Beech saplings between 10 and 20 cm show similar relationship with CWD and stone, furthermore weak negative correlation with percent of living canopy tree stems (tree) and diffuse light (DIF PACL). Larger *F. sylvatica* and *S. caprea* saplings are in positive correlation with total cover of herbaceous species (plantsum) and percent of intact soil. *Salix* also seems to have positive relationship with diffuse light.

Table 3. Results of correlation analysis between number of tree individuals and abiotic variables in 2004. (Explanation in the text.)

Seedling species and size (cm)	CWD (n=355)	stone (n=355)	tree (n=355)	intact soil (n=355)	plantsum (n=355)	DIF PACL (n=44)
F. sylv. < 10	R=-0.15***	R=0.15***				
F. sylv. 10-20	R=-0.15***	R=0.14***	R=-0.12**			R=-0.29**
F. sylv. 20-50			R=-0,11**	R=0,15***	R=0,20***	
S. capr.10-50			R=-0,11**	R=0,16***	R=0,31***	R=0,38**

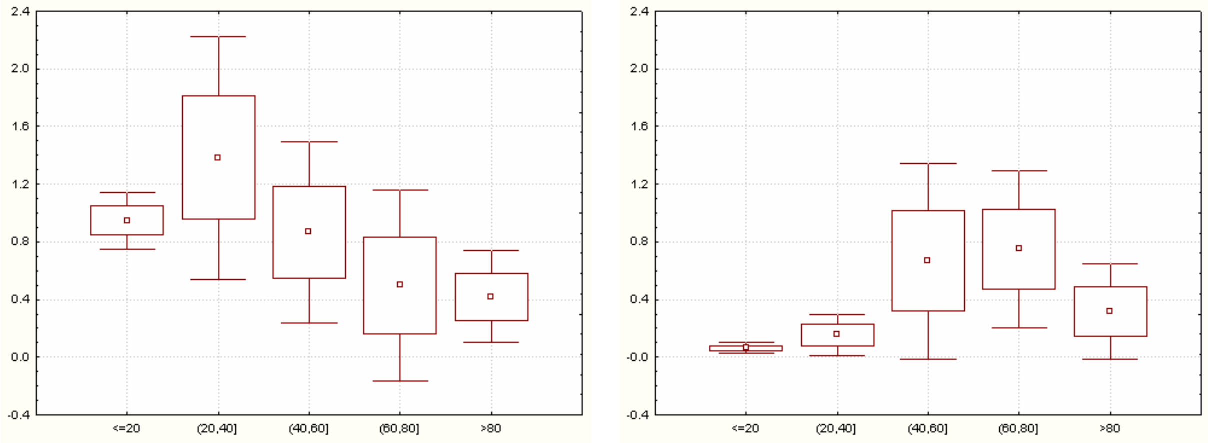
In 2002 most *Salix caprea* saplings belonged to small size classes (<20 cm). Plots where *Salix* was present can be characterized by significantly (Mann-Whitney U Test, p<0.1) lower percent of intact soil compared to those where *Salix* did not occur. On the contrary, in 2004 larger saplings (> 20cm) became dominant, *Salix* saplings were found especially in quadrats where intact soil is more characteristic *(Figure 8)*.



(a) (b)

*Figure 8. Percent of intact soil per quadrat according to the occurrence of Salix caprea saplings in 2002 (a) and in 2004 (b). 0: plots where Salix does not occur, 1: plots where Salix occurs, Centre of the box represents mean, box represents ± 1*SE, whisker represents ± 2*SE)*

Each size class of *Fagus sylvatica* shows different distribution according to total cover of herbaceous species *(Figure 9.)* in 2004. Small seedlings (<10 cm) are most abundant at 20-40% of total cover, while amount of larger saplings (20-50 cm) increases with total cover and reaches maximum values at 60-80 %. Higher herbaceous cover does not seem to be preferred by seedlings and saplings. *Salix caprea* shows similar distribution as higher beech saplings *(Figure 10)*.



(a) (b)

Figure 9. Average number of Fagus sylvatica saplings (0-10 cm (a); 20-50cm (b)) according to total cover of herbaceous species (plantsum) in 2004. (Signs as in figure 8)

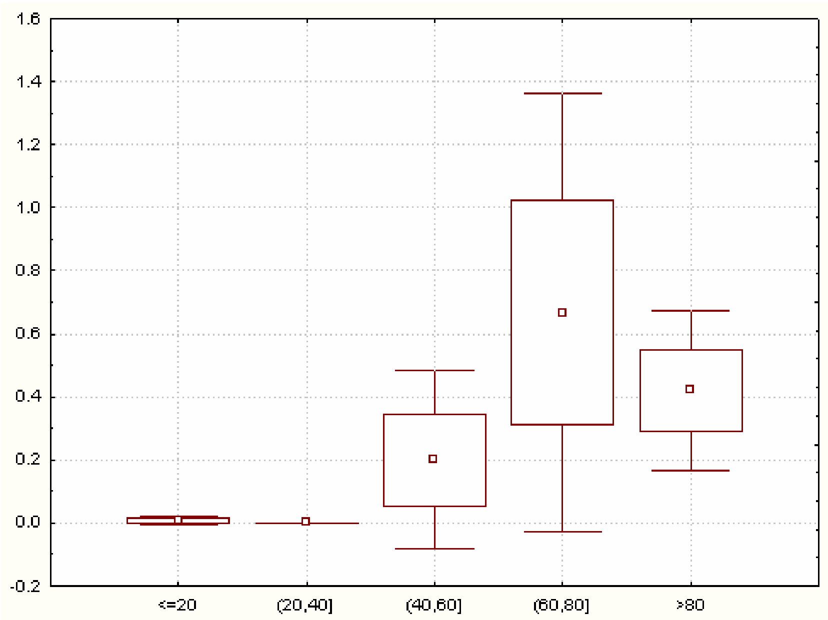


Figure 10. Average number of Salix caprea saplings according to total cover of herbaceous species (plantsum) in 2004. (Signs as in figure 8)

4 DISCUSSION

Our results show considerable overall increases in light levels in gaps. It is similar to previous studies in temperate forests that found that light quantity increases with opening size (Canham *et al* 1990 and references therein, Collins and Pickett 1987, 1988). It is necessary to emphasize that beside changes in light conditions, increase of soil water content is also a characteristic process after gap formation according to other studies (Collins et al. 1985, Minckler and Woerheide 1965, Pontailler 1979). Our other investigations also showed (Mihók et al. 2004) that the measured water content values in the gaps, at the edges of the gaps and below the closed canopy are similarly different, regardless of the gap size. The increase of soil water content in gap centres may also have an essential effect on tree regeneration processes.

Preliminary results of our long-term investigations suggest, that opening of artificial gaps facilitated growth of newly established seedlings, beside advance regeneration that was present before gap creation. There was a mast year for beech in 2001, which increased the amount of regeneration mainly in two gaps in the following years.

While in the case of the small gaps there is no difference between in-gap and under-canopy position, average number of small beech seedlings is lower in the centre of large gaps than under canopy, which is explained by some authors (Peltier et al. 1997) as dispersal limitation. Larger beech saplings are more abundant in the centre of large gaps and *Salix,* as well, occurs more in central plots of large gaps. Occurrence of shade intolerant tree species with significant ability of dispersal in centres of large gaps is reported from different forest types (Lawton 1990).

Our results show that the establishment of *Fagus* seedlings is quite insensitive to environmental conditions. Germination is not influenced by light, – where seed dispersal is effective, i.e. in smaller gaps – the probability of establishment of *Fagus* seedlings is the same in gaps and under canopy (Muys et al. 1988, Hahn 2000). Success of establishment depends more on soil moisture than on light conditions (Fanta 1995). Large amount of coarse woody debris, however, seems to make establishment difficult. Dense slash and stems may inhibit seeds to reach ground surface leading to high seed mortality. Stones, however, may provide appropriate refugia for seeds against seed predators, but further investigations would be necessary to make this relationship clear.

On the contrary, older *Fagus* saplings showed positive relationship with increasing herbaceous cover. Taller saplings were present mainly in the center of large gaps. Higher herbaceous abundance is due to increased incident light – and other factors e.g. soil water content. Though larger saplings did not show significant correlation with relative light intensity according to our results, other studies (Peltier et al. 1997) indicate that light is very important factor for sapling development, enhancing especially root development. In poor light conditions, seedlings are more susceptible to drought (Topoliantz and Ponge 2000). We suggest that the result – larger saplings occur in centre of large gaps, where herbaceous cover is dense – can also be related to game damage. In the dense herb layer developing in gaps, herbivores may not find every seedling, so saplings may survive with bigger chance – this effect may be in trade off with the competitive pressure of increasing herb cover. This finding is supported by other studies focusing on the effect of density and height of neighbouring vegetation on tree sapling susceptibility (Miller et al. 1982, Gill 1992, Rao et al. 2003, Pietrzykowski et al. 2003 and references therein, Kuiters and Slim 2003). Further investigations would help to get a better understanding of gap regeneration processes and its applicability in forestry practice.

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